

A NEW GOOSE FROM THE LATE PLIOCENE OF NEBRASKA WITH NOTES ON VARIABILITY AND PROPORTIONS IN SOME RECENT GEESE

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ABSTRACT: A nearly complete but moderately crushed skeleton of a late Pliocene (Blancan) goose from the Broadwater Local Fauna of western Nebraska is described and named as *Anser thompsoni* new species. This rather large goose was larger than Recent *Anser caerulescens* (Linnaeus) and smaller than the larger races of Recent *Branta canadensis* (Linnaeus). Particularly distinctive characters include a relatively short bill and a relatively very small furcula. The wing resembled *Anser caerulescens* and *Anser rossii* Cassin in its relatively long ulna. The leg was relatively short as in Recent *Anser albifrons* (Scopoli) and *Branta canadensis*.

Among Hildegard Howard's many contributions to avian paleontology is her excellent review (1964) of the fossil anseriforms, in which she lucidly considered the strengths and weaknesses of the fossil record of waterfowl and summarized all that was then known. This has been helpfully supplemented by Woolfenden's (1961) thorough study of the qualitative osteology of modern anseriforms.

We have recently begun to study the fossil birds of the Blancan Broadwater Local Fauna of western Nebraska. Most of these are water birds, including a remarkably complete skeleton of a goose that appears to represent a new species of the widespread Holarctic genus *Anser* Brisson.

The completeness of this specimen provided the rare opportunity for a fairly accurate reconstruction of the body proportions of a fossil species. Comparing these with those of Recent geese, however, posed problems. Although Verheyen (1955a, 1955b) has extensively surveyed the rather variable proportions of Recent geese, his sample sizes (one or two, rarely up to four specimens per species) provide little indication of the limits and nature of variation. For comparative purposes we have therefore been obliged to undertake a limited analysis of the relevant aspects of variation in several Recent geese presently represented by major populations in interior North America.

The description of this unusually complete fossil seemed especially appropriate for the present volume in recognition of Howard's long interest in and study of fossil waterfowl and in appreciation of her often stated and intelligently tempered concern (e.g., Howard 1964:235-237) about the problems posed in study of often fragmentary individual specimens.

Only two Blancan local faunas have extensively studied avi-

faunas: the Rexroad Local Fauna (*sensu lato*) and the Hagerman Local Fauna. Feduccia (1975) has summarized the information pertaining to birds for these two faunas. Other Blancan sites are probably also rich in bird material; this is certainly true of the Broadwater Local Fauna (for correlation chart see Schultz and Martin 1977), which is one of the least studied.

In addition to the birds, the Broadwater Local Fauna has a large mammalian component (list modified from Schultz and Stout 1948:563-564): *Sorex* sp. (shrew), *Paramylodon* sp. (ground sloth), *Megalonyx* sp. (ground sloth), *Hypolagus* sp. (rabbit), *Spermophilus* sp. (ground squirrel), *Paenemarmota barbouri* Hibbard and Schultz (giant ground squirrel), *Geomys* sp. (pocket gophers), *Procastoroides sweeti* Barbour and Schultz (giant beaver), *Castor* sp. (beaver), *Peromyscus* sp. (white-footed mouse), *Neotoma* sp. (wood rat), *Pliopotamys meadensis* Hibbard (Extinct muskrat), *Pliophenacomys* sp. (extinct vole), *Pliozapus?* sp. (jumping mouse), *Canis lepophagus* Johnston (extinct coyote), *Borophagus diversideus* (Cope) (extinct canid), *Satherium piscinaria middleswarti* Barbour and Schultz (extinct otter), *Lutravis* sp. (extinct mustelid), *Ischorosmilus crusifonti* Schultz and Martin (scimitar-toothed cat), *Stegomastodon mirificus* (Leidy) (short-jawed mastodon), *Pliomastodon* sp. (ancestral American mastodon), *Equus (Dolichohippus) simplicidens* (Cope) (extinct horse), *Nannippus* sp. (extinct horse), *Platygonus* sp. (peccary), *Camelops* sp. (extinct camel), *Tanupolama* sp. (extinct camel), *Titanotylopus spatulus* (Cope) (giant camel), *Capromeryx arizonensis schultzi* Skinner (ancestral pronghorn).

The presence of the more advanced muskrat *Pliopotamys meadensis* in the Broadwater Local Fauna and of the less advanced *P. minor* in the Hagerman Local Fauna suggests that the Broadwater is the younger of the two. These faunas are near the age of, or somewhat younger than, the earliest evidence of extensive continental glaciation (Boellstorff 1976; Mercer 1978), approximately 3.5 million years ago.

The Broadwater fossils come from unconsolidated sands and

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fine-grained silts that were deposited in or adjacent to a large Pliocene river system. The goose skeleton was found in the "marly" facies, suggesting an area of local ponding. In association with it were many specimens of the extinct muskrat *Pliopotamys* Hibbard, and it probably also shared its habitat with the giant aquatic beaver *Procastoroides* Barbour and Schultz and the extinct river otter *Satherium* Gazin.

MATERIAL

In addition to the fossil (see Systematics section), the material studied consisted of relevant specimens from the neosteological collections of the University of Kansas Museum of Natural History, Division of Birds. Available was a series of 17 male and 12 female "lesser" Snow Geese from Kansas and Missouri (*Anser caerulescens caerulescens* (Linnaeus)), migrant representatives of the population breeding on the southwestern shore of Hudson's Bay (Palmer 1976:137, 140). These provided a comparatively good picture of variability in a fairly homogeneous population of modern geese. Also available were a good series (7 males, 8 females) of Ross's Goose (*Anser rossii* Cassin), a heterogeneous assemblage of Canada Geese (*Branta canadensis* (Linnaeus)), including 8 sexed examples of several of the larger subspecies and several additional specimens of the smaller ones, 3 Brant (*B. bernicla* (Linnaeus)), and 2 White-fronted Geese (*A. albifrons* (Scopoli)). These were supplemented by a loan of selected elements of a Greylag (*A. anser* (Linnaeus)) and a Bean Goose (*A. fabalis* (Latham)) from the National Museum of Natural History, Smithsonian Institution, and measurements taken for us in that museum of 3 additional Canada Geese and 3 more White-fronted Geese.

Because of the nature and preservation of the fossil's elements, the literature proved adequate for consideration of the fossil forms that seemed relevant, primary sources being almost all at hand, as well as having been conveniently summarized by Howard (1964).

Terminology is that of Howard (1929). All measurements were taken to the nearest 0.1 mm with dial calipers.

SYSTEMATICS

Order Anseriformes

Family Anatidae—Ducks, Geese, and Swans

Genus *Anser* Brisson 1760

Anser thompsoni new species

Figures 1–4

HOLOTYPE: Most of a skeleton UNSM (University of Nebraska State Museum) 1110, including skull, furcula, coracoid, humerus, carpometacarpus, tibiotarsus, and other elements. Collected in 1939 by Joseph Johnson.

LOCALITY AND HORIZON: Broadwater Quarry 4 (NE ¼, Sec. 20, T.19N., R.47W.—on the Dan Bowman ranch, 8.4 km E and 1.2 km N of Broadwater, Morrill County, Nebraska), from the Lisco Member, Broadwater Formation, late Pliocene (Blancan). A cast of this specimen is on deposit at the University of Kansas Museum of Natural History (KU 24669).

DIAGNOSIS: A moderately large goose, smaller overall than the larger subspecies of modern *Branta canadensis* but larger than any known subspecies of *Anser caerulescens* or *A. albifrons*.

Compared with all other geese examined, *Anser thompsoni* is characterized by having bill from fronto-nasal hinge to tip shorter in relation to skull length (total length/bill length 2.13; 1.87–1.97 in Recent geese seen). Posterior rami of lower jaw deeper.

Furcula relatively very small.

Humerus with impression of *M. brachialis anticus* more elongate and more nearly parallel with the shaft; attachment of anterior articular ligament nearly circular (oval in all other geese examined); pectoral attachment not extending as far anteriorly.

Carpometacarpus with the process of metacarpal I longer and narrower, with its proximal edge angling proximad (as opposed to vertically or distally); distal metacarpal symphysis relatively and absolutely longer.

Tibiotarsus with the tendinal foramen beneath the supratendinal bridge circular rather than oval, and the groove for *M. peroneus profundus* relatively broad, shallow, and short.

MEASUREMENTS (in mm): Skull: from postermost point of supraoccipital to fronto-nasal hinge (articulation with beak) 63.9; beak from this point to tip 56.4 (total 120.3). Lower jaw: depth of right mandibular ramus at posterior margin of coronoid process 14.4. Coracoid (left): anterior end of brachial tuberosity to middle of furcular facet 68.4. Humerus: total length 167.0 (left); greatest width near head, at right angles to shaft 36.3 (right). Ulna (left, on slab): estimated length 166 ± 1 (the olecranon process and the condyles are somewhat eroded). Carpometacarpus (left): total length 97.8; apex of process of metacarpal I to posterior margin of internal carpal trochlea 23.7. Proximal phalanx of digit II: length 40.0. Second phalanx of digit II: length 27.2. Femur (left, on slab): estimated length 83 ± 1. Tibiotarsus (left): length from external condyle to proximal articulating surface (i.e., exclusive of cnemial crests) 133.9; width across condyles 15.5; greatest anteroposterior depth between condyles 11.0. Tarsometatarsus (right, on slab): length 90.3.

ETYMOLOGY: *Anser thompsoni* is named for Max Clyde Thompson, Southwestern College, Winfield, Kansas, in grateful recognition of his many contributions to the bird collection of the University of Kansas Museum of Natural History, including its extensive osteological component.

DESCRIPTION: UNSM 1110 is a nearly complete, but moderately crushed skeleton (Fig. 1). Crushing, while not affecting most of the articular surfaces, has generally flattened the shafts of the long bones, precluding meaningful measurements of their diameters. The bones, while associated, are generally not in precise articulation. The general orientation is with the left side up. The head and neck are extended and the limbs are folded into a mass, rendering their removal and study difficult. The humeral end of the right coracoid and a fragment of the synsacrum have been displaced to the region of the head. While the sternum is missing, the undamaged furcula is nearly in correct anatomical position. The relationship of the elements is not inconsistent with the notion that the breast, viscera, and hip region were removed by some predator prior to burial.

Present in some form are all of the long bones; the shoulder girdle lacking the sternum; and the skull, lower jaw, and many of the cervical vertebrae. The synsacrum is missing, except for the above-mentioned fragment (which was removed from the slab (Fig. 1) before the photograph was taken), as are most of the ribs. The following elements, at least one of nearly every



Figure 1. The holotype, UNSM 1110, of *Anser thompsoni* new species approximately as it appeared in situ.

one successfully removed from the matrix and associated bones, are sufficiently well preserved to permit meaningful comparisons.

Skull. This is crushed and flattened in a plane between vertical and horizontal, but considerable detail is preserved, especially on the under (right) side (Fig. 2). In every respect it resembles *Anser* rather than *Branta*. The relative size is comparable to the present-day Snow Goose, but the bill is decidedly short relative to total length. Nareal opening ovoid, relatively short and broad, like *A. caerulescens* rather than *B. canadensis*. Profile of forehead and proximal bill straight as in living species of *Anser* (concave in *B. canadensis*); supraorbital region not noticeably excavated as in *Anser* (in *B. canadensis* this is moderately excavated, presumably for a nasal gland); orbit large and lachrymal short and broad as in *Anser*; lateroventral margin of maxilla moderately arched as in *A. caerulescens* and *A. albifrons* (it is nearly straight in *B. canadensis*). (The so-called "grin patch" on the bill of the Recent Snow Goose appears to be a ramphothecal feature and not an osteological one.)

Lower jaw. Rami short and massive (Fig. 2) with the posterior portion deeper than in other geese examined. Dentary

curved as in *Anser caerulescens*. Coronoid process with a straight anterior margin as in *A. caerulescens* and *A. albifrons*, and a gently sloping posterior margin as in *Branta canadensis* and *A. caerulescens* (*A. albifrons* has a more abruptly curving posterior coronoid margin). Posterior margin of dentary below the lateral process of the surangular as in *Anser* (anterior to the lateral process in *Branta*).

Cervical vertebrae. These suggest a neck of average length for a species of *Anser* of comparable size. A number are missing; only 10 are visible on the slab. Recent species of *Anser* have 18, 19, or 20 (Verheyen 1955b:10–11).

Furcula. Somewhat warped and distorted, the furcular rami of *Anser thompsoni* are relatively thick, relatively short, and relatively uncurved anteroposteriorly. Somewhat surprisingly, the wishbone was clearly smaller than those of Recent *A. caerulescens*, which is considerably smaller than the fossil in other measurements; it is little larger than that of a large *A. rossii*. In short, the fossil seems to have had a remarkably small furcula, indeed, relative to Recent geese examined. Qualitatively the element seems closest to that of *A. albifrons*. (The furcula of *Branta canadensis* differs from all of those discussed

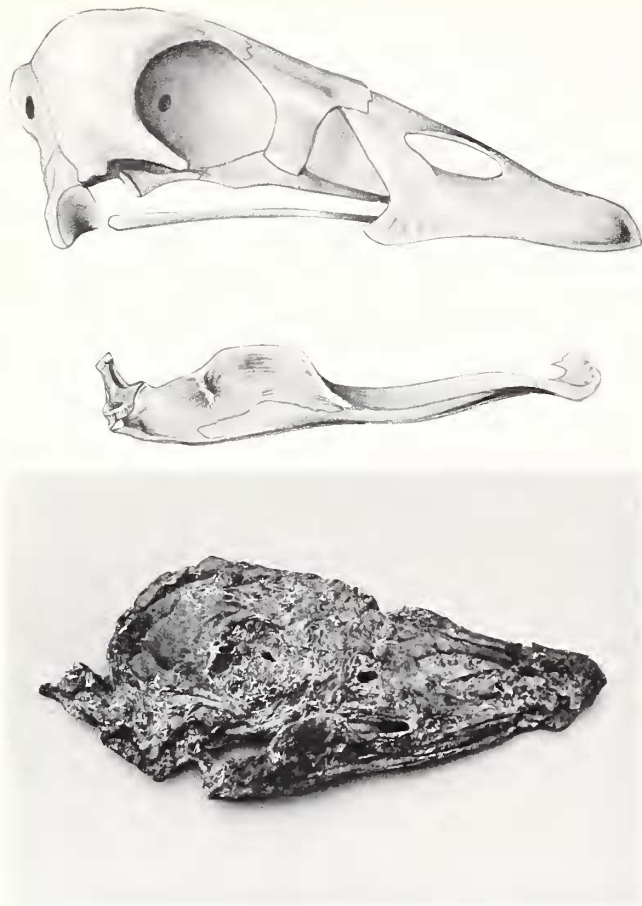


Figure 2. Upper, restoration of the skull and lower jaw of *Anser thompsoni* new species ($\times 3/4$). Lower, right side of the skull of the holotype of *Anser thompsoni* new species.

in having the rami relatively long and set comparatively close together.)

Scapula. The one scapula present is robust in comparison with those of other geese examined and its pneumatic foramen is relatively very small. The posterior end is missing.

Coracoid. As do all of the living species of *Anser*, *A. thompsoni* has, just posterior to the brachial tuberosity, a distinct fossa that contains pneumatic foramina (Fig. 3b). However, the foramina are not as large and numerous as they are in modern species of *Anser*. In *Branta canadensis* (and its diminutive relative *B. bernicla*), the size and number of pneumatic foramina reaches an extreme; the whole furcular facet is generally undercut with pneumatic foramina along its entire posterior margin (noted by Woolfenden 1961:49). In *A. thompsoni* the furcular facet is less depressed than in *A. caerulescens*. The procoracoid is short and blunt, and the glenoid facet is narrow and *Anser*-like (less nearly circular than in *Branta*). Breakage precludes measurement of its greatest length, but the coracoid is relatively long, approximately equal to that of *B. canadensis* specimens that are considerably larger in most other dimensions.

Humerus. Humeri badly crushed but entire (Fig. 3c). They appear to have been robust. Impression of M. brachialis anticus more elongate and more nearly parallel to the shaft than in other geese examined (one specimen of Old World *Anser*

anser approaches it in this respect); attachment of anterior articular ligament nearly circular (oval in other geese, so that its proximal border extends well proximad to the external condyle); ectepicondyle narrow as in *A. caerulescens*; pectoral attachment does not project as far anconad as in other geese; pneumatic foramen (proximal end) small and capital groove relatively small.

Ulna. The left ulna, exposed on the slab, possesses no relevant features other than length sufficiently intact for comparisons.

Carpometacarpus. Relatively rather long (Fig. 3a). Internal carpal trochlea does not project as far beyond the plane of metacarpal III as in Recent geese; internal ligamental fossa more nearly circular (less oval) than in other geese studied; process of metacarpal I longer and narrower than in modern geese, its proximal profile angling proximad (it angles vertically or posteriad in living geese); extensor attachment relatively large (resembling *Branta esmeralda* Burt in these particulars); distal metacarpal symphysis longer, absolutely and relatively, than in other geese examined.

Proximal phalanx, digit II. Comparatively large and broad, not as elongate, relatively, as in *Branta*, but too badly crushed to make detailed comparison useful.

Distal phalanx, digit II. This element resembles the comparable one in *Anser caerulescens*.

Femur. Still attached to slab. Imperfect and badly crushed but comparatively large and (though not precisely measurable) at least as long as that of a fairly large specimen of *Branta canadensis*, which is considerably larger in most other dimensions.

Tibiotarsus. Distal end and about two-thirds of the shaft of the left tibiotarsus present (Fig. 4a). The proximal end, badly crushed, could not be saved during removal; however, the total length was ascertained. The element is relatively very short. Also of interest is the shape of the distal articular surface when viewed end-on. In *Anser thompsoni* and *A. caerulescens* it is more compressed than in *Branta canadensis* and *A. albifrons* (the width across the condyles divided by the depth of the shaft between them in randomly selected specimens gives ratios of 0.61 in *B. canadensis*, 0.63 in *A. albifrons*, and 0.72 in both *A. caerulescens* and *A. thompsoni*). That this feature is rather variable among living geese, however, is indicated by ratios of 0.69 and 0.79 respectively for single specimens of *A. fabalis* and *A. anser*. The tendinal foramen beneath the supratendinal bridge is circular in *A. thompsoni*, rather than oval as in other geese. The external condyle is relatively rounded, and the groove for M. peroneus profundus is relatively broad, shallow, and short.

Tarsometatarsus. Relatively elongate as in *Anser caerulescens* (Fig. 4b). Detailed characters not well preserved.

DISCUSSION

COMPARISONS WITH EXTINCT TAXA

No extinct goose seems particularly close to *Anser thompsoni* on the basis of available evidence. The fossil species of greatest chronological and systematic relevance are represented by only one or a few elements (some of them referred to these species by later workers), most of which are not directly comparable.

Nearest in age is *Anser pressus* Wetmore (1933), known by a femur (length 66.9 mm) from the Hagerman Lake Beds

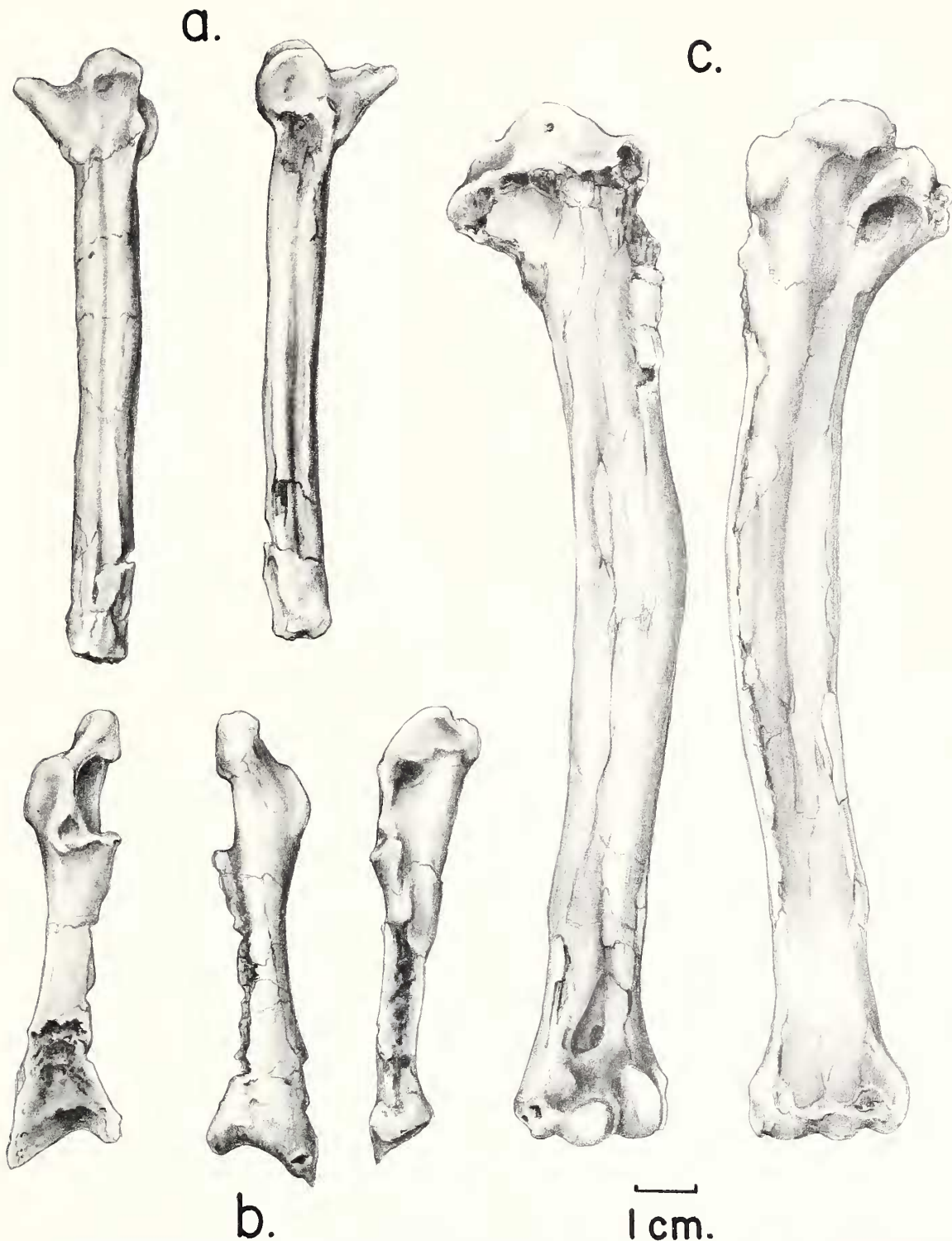


Figure 3. Some elements of the holotype of *Anser thompsoni* new species ($\times 1$). a, left carpometacarpus, in internal and external view. b, left coracoid, in dorsal, ventral, and internal view. c, left humerus, in palmar and anconal view.

(Blancan) of Idaho. Although the crushed condition of the present specimen prevents comparisons other than in size, *A. thompsoni* was a much larger bird (femur approximately 83 mm). It was also much larger than *Branta propinqua* Shufeldt (1892) from the late Pleistocene of Oregon (humerus 106.2 versus 167.0 mm) and *B. esmeralda* Burt (1929) from the Miocene

of Nevada (carpometacarpus 77.6 versus 97.8 mm). The latter species also seems to have had a relatively shorter carpometacarpus. The shape of the process for digit II is similar in *A. thompsoni* and *B. esmeralda*. *Eremochen* Brodkorb and *Heterochen* Short (Brodkorb 1961:174; Short 1970) are distinctive extinct genera that do not appear to be closely similar to *Bran-*

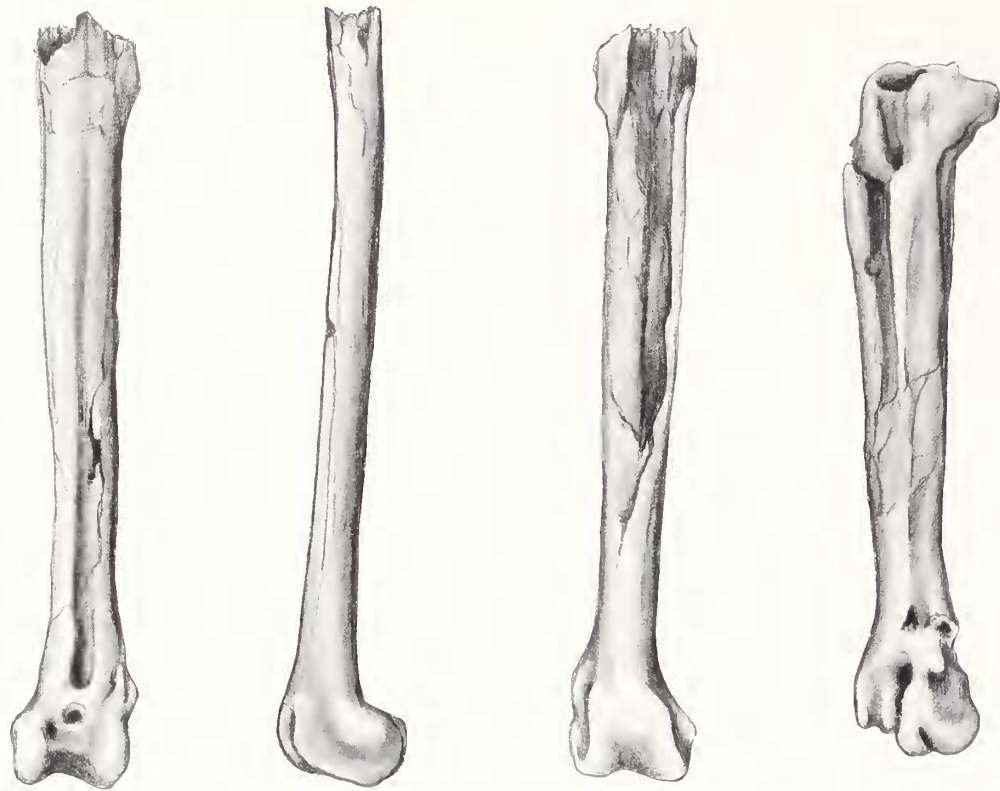


Figure 4. Some elements of the holotype of *Anser thompsoni* ($\times 1$). From left to right: anterior, internal, and posterior view of left tibiotarsus and left tarsometatarsus, posterior view.

ta or *Anser. Presbychen abavus* Wetmore (1930) from the Miocene of California and *B. dickeyi* L. Miller (1924) from the Pleistocene of California and Oregon are giant species much larger than *Anser thompsoni*. *Anser equitum* Bate (1916), from the late Pleistocene of Malta, if all its elements belonged to the type, was a weirdly proportioned bird perhaps incapable of flight. *Branta howardae* L. Miller (1930) from the late Miocene is based solely on the distal end of a carpometacarpus and few comparisons are possible. The distal metacarpal symphysis, however, is shorter than that of *A. thompsoni*. *Anser azerbaijdzhanicus* Serebrovsky (1940), from the Pleistocene of Azerbaijan, USSR, apparently had a much larger cranium and more bulging frontals (see Howard 1964:269).

COMPARISONS WITH RECENT TAXA

Most if not all living geese have been recorded from the Pleistocene and one or two from earlier time (Brodkorb 1964:234–237). Recent workers are increasingly reluctant, however, to credit the existence of living species before the Pleistocene (Brodkorb 1966; Feduccia 1975). Although *Anser thompsoni* shares osteological characters with various living geese (see Systematics section), several are diagnostic, individually or in combination. Features of the carpometacarpus alone separate it from Recent forms.

Because fossil remains of birds usually consist of a few elements at most, these often fragmentary, comparisons are generally restricted to a few characters and often to relative estimates of general size. The relative completeness of *Anser*

thompsoni, however, permits unusually extensive comparison, at least with Recent geese (Tables 1 and 2).

SOME STATISTICAL CONSIDERATIONS: A full-scale statistical study of proportions in modern geese, while much to be desired, is far beyond the scope of this paper. Although we restricted ourselves to readily available samples of the living geese presently numerous in continental North America, we think we have gained some insights into the probable range of dimensions in *Anser thompsoni* and its general proportions compared with some familiar living forms. A few explanations are necessary.

1. A modest, but significant, sexual difference in size required that males and females of both *A. caerulescens* and *A. rossii* be separated in statistical analysis of direct measurements (Table 1). Sexes of *Branta canadensis* and *A. albifrons* were not so separated because the sample of the former included several of the larger subspecies, while that of the latter consisted of unsexed individuals. Hence both would be expected to show exaggerated variances.

2. We combined sexes when considering relative proportions (ratios) because there was no evidence of significant sexual dimorphism in any of these species. This improved the sample sizes (Table 2).

3. Ratios, individually determined for each specimen and summed, were treated statistically in the same way as (more or less) normally distributed linear measurements. Although numerous precedents exist in similar cases (e.g., Engels 1940 and citations therein), caution is required (Simpson, Roe, and Lewontin 1960:163–165; Sokal and Rohlf 1969:17–18). In the

Table 1. Measurements (in mm) of various geese with means $\pm$ standard errors, standard deviations, and N (*Anser caerulescens*, *A. rossii*); or mean, N, and range (*Branta canadensis*, *A. albifrons*).*

Character	<i>Anser thompsoni</i> (new species)	<i>Anser caerulescens</i>	<i>Anser rossii</i>	<i>Branta canadensis</i> (large races)	<i>Anser albifrons</i>	<i>Anser anser</i>	<i>Anser fabalis</i>
Skull + bill	120.3	♂♂ 116.3 $\pm$ 0.7 2.6 (15) ♀♀ 111.8 $\pm$ 1.3 3.6 (8)	♂♂ 86.2 $\pm$ 0.7 1.8 (7) ♀♀ 83.7 $\pm$ 1.4 3.7 (8)	120.5 (10) 116.2–128.9	105.6 (5) 102.2–110.2	—	—
Bill	56.4	♂♂ 61.8 $\pm$ 1.3 5.2 (15) ♀♀ 58.0 $\pm$ 0.4 1.0 (8)	♂♂ 44.4 $\pm$ 0.3 0.9 (7) ♀♀ 42.7 $\pm$ 1.0 2.6 (8)	63.2 (7) 56.9–69.0	56.9 (2) 55.2, 58.5	—	—
Humerus	167.0	♂♂ 148.3 $\pm$ 1.2 4.9 (17) ♀♀ 144.0 $\pm$ 1.1 3.9 (12)	♂♂ 128.0 $\pm$ 0.9 2.2 (6) ♀♀ 124.4 $\pm$ 1.5 3.9 (8)	181.8 (11) 168.6–194.9	147.9 (5) 143.8–152.7	117.6 (1)	161.4 (1)
Ulna	166 $\pm$ 1 (estimate)	♂♂ 148.3 $\pm$ 1.2 4.9 (17) ♀♀ 143.5 $\pm$ 1.3 4.4 (12)	♂♂ 127.3 $\pm$ 1.3 3.3 (7) ♀♀ 124.0 $\pm$ 1.7 4.1 (7)	171.8 (11) 157.3–182.6	143.0 (5) 138.3–146.2	—	—
Carpometacarpus	97.8	♂♂ 83.1 $\pm$ 0.9 3.5 (16) ♀♀ 80.0 $\pm$ 0.7 2.5 (12)	♂♂ 73.4 $\pm$ 0.9 2.4 (7) ♀♀ 70.4 $\pm$ 0.7 1.9 (8)	101.1 (10) 92.9–104.8	83.1 (5) 78.9–84.7	98.5 (1)	91.3 (1)
Femur	83 $\pm$ 1 (estimate)	♂♂ 73.0 $\pm$ 0.7 2.8 (17) ♀♀ 71.1 $\pm$ 0.3 1.2 (12)	♂♂ 62.5 $\pm$ 0.5 1.2 (7) ♀♀ 61.0 $\pm$ 0.8 2.1 (8)	84.1 (8) 77.8–91.9	71.1 (2) 68.4, 73.9	—	—
Tibiotarsus	133.9	♂♂ 132.5 $\pm$ 1.3 5.3 (17) ♀♀ 129.9 $\pm$ 1.1 3.8 (12)	♂♂ 114.2 $\pm$ 0.9 2.3 (7) ♀♀ 113.2 $\pm$ 1.1 3.0 (8)	148.6 (11) 140.7–159.8	121.7 (5) 118.7–124.2	149.6 (1)	133.4 (1)
Tarsometatarsus	90.3	♂♂ 84.0 $\pm$ 1.1 4.7 (17) ♀♀ 80.9 $\pm$ 0.7 2.6 (12)	♂♂ 71.6 $\pm$ 0.5 1.2 (7) ♀♀ 68.8 $\pm$ 1.5 3.9 (8)	90.9 (11) 83.6–98.8	72.4 (5) 70.6–74.5	91.9 (1)	72.9 (1)

* The abridged statistical treatment of *B. canadensis* and *A. albifrons* is explained in text.

present case, although the distributions of our ratios somewhat resemble normal ones (their coefficients of variation average somewhat smaller than those of the direct measurements), we regard their confidence limits with some suspicion and have avoided firm conjectures except where differences and *t* values were considerable.

GENERAL SIZE: Relations among the Recent taxa and their elements are observable in Table 1. Standard deviations in populations of equal variability are directly proportional to size (i.e., the mean). Thus, in comparing the fossil with Recent geese, one may infer the standard deviation (Fisher 1952) of a single specimen from that of a near relative (e.g., *Anser caerulescens*, assuming similar variability) and plot the theoretical ranges of its population within any chosen limits (here $\pm 2\sigma$ or 95 percent of a theoretically normal population). This may be done considering the single specimen either as an average, a very small, or a very large example (Simpson, Roe, and Lewontin 1960:207–208). The results, for the absolute size of the fossil humerus compared with that of the Snow Goose, are shown in Figure 5a.

Clearly, if the holotype of *Anser thompsoni* is a relatively very large example, the measurements of its population would extensively overlap those of male *A. caerulescens* and other geese of comparable size.

In short, while there is no question that *Anser thompsoni* (humerus length 167 mm) averaged very much to considerably larger than *A. caerulescens* (mean length of humerus, ♂♂, 144 mm), even given the seemingly large difference of 23 mm (16 percent above the Snow Goose mean), very extensive overlap of *individuals* is not ruled out. This assumes particular importance whenever size is the only meaningful character in a comparison, and is especially worth noting among geese, which are usually polytypic and often highly so (individual Canada Geese from various populations range from 1.3 to more than 10 kg in weight).

PROPORTIONS: Of special interest here are ratios involving the limbs and their components (Table 2), characters related to locomotion. *Anser thompsoni* lacks any conventional index of "absolute" body size (e.g., trunk length, Engels 1941:63), so we have expressed the lengths of appendicular

Table 2. Proportions of various geese (as percent) with means $\pm$ standard errors, standard deviations, and N.

Character (Ratios of lengths)	<i>Anser thompsoni</i> (new species)	<i>Anser caerulescens</i>	<i>Anser rossii</i>	<i>Branta canadensis</i> (large races)	<i>Anser albifrons</i>	<i>Anser anser</i>	<i>Anser fabalis</i>
Skull/bill	213.2	190.3 $\pm$ 2.0 8.5 (23)	196.8 $\pm$ 1.6 5.7 (11)	192.0 $\pm$ 2.2 5.8 (7)	186.9 (2) 186.5, 187.3	—	—
Ulna/humerus	99.4 (estimate)	100.0 $\pm$ 0.5 2.8 (29)	99.0 $\pm$ 0.7 2.6 (11)	94.5 $\pm$ 0.4 1.2 (11)	96.7 $\pm$ 0.7 1.6 (5)	—	—
Carpometacarpus/humerus	58.6	55.9 $\pm$ 0.2 1.0 (28)	56.7 $\pm$ 0.2 0.5 (12)	56.0 $\pm$ 0.3 0.8 (10)	56.2 $\pm$ 0.6 1.2 (5)	55.5 (1)	56.6 (1)
Femur/humerus	49.7 (estimate)	49.4 $\pm$ 0.5 2.5 (29)	48.8 $\pm$ 0.2 0.7 (12)	46.4 $\pm$ 0.4 1.2 (8)	48.2 (2)	—	—
Tibiotarsus/humerus	80.2	89.9 $\pm$ 0.4 1.9 (29)	90.0 $\pm$ 0.5 1.8 (12)	81.6 $\pm$ 0.5 1.7 (11)	82.3 $\pm$ 0.8 1.8 (5)	84.2 (1)	82.7 (1)
Tarsometatarsus/humerus	54.1	56.5 $\pm$ 0.3 1.5 (29)	55.2 $\pm$ 0.4 1.3 (12)	50.0 $\pm$ 0.5 1.7 (11)	48.9 $\pm$ 0.5 1.1 (5)	51.7 (1)	49.5 (1)
"Index of locomotion"	140.2 (estimate)	130.7 $\pm$ 0.5 3.0 (28)	131.7 $\pm$ 0.7 2.2 (11)	140.4 $\pm$ 1.5 3.8 (7)	141.0 (2) 141.0, 141.0 145**, 146**	142**	141**
Humerus/trunk	—	77.6 (5)	80.6 (2)	76.6 (2)	79.4 (2)	—	—

* Humerus + Ulna + Carpometacarpus/Femur + Tibiotarsus + Tarsometatarsus.

** From Verheyen, 1955b.

elements as percentages of the length of the humerus. This element has been found to be a fair indicator of general body size in comparatively homogeneous groups of anseriforms (Humphrey and Clark 1964:189).

In assessing the validity of the humerus as an indicator of absolute size, we measured the trunk lengths of a few of the Recent geese in our samples and obtained humerus/trunk length ratios (Table 2). The differences found between species in these small samples are uniformly insignificant ($p < 0.20$ to 0.40). Trunk length is difficult to measure even in articulated specimens and prohibitively difficult in disarticulated ones.

For present purposes, therefore, we accept the humerus as at least a moderately good standard of overall size in these geese. Even if it were not, the ratios presented here provide direct intramembral ratios for wing elements and standardized, indirect ones for hind limb elements and intermembral comparisons. As such, all of them are directly comparable among the species considered.

Three sets of relationships are of special interest.

1. The length of the hind limb and its elements. *Anser cae-*

rulescens and *A. rossii*, virtually sibling species, are distinctly long-legged geese. This is clearly perceptible in the field when the birds are standing. The "index of locomotion" (i.e., wing length/leg length; see Verheyen 1955b:10–12) for *A. caerulescens* compared with *Branta canadensis* in the present samples shows this very clearly ($p < 0.001$). *Anser thompsoni* differs from *A. caerulescens* in this respect, being short-legged like the Canada Goose ($0.001 < p < 0.01$), a difference also revealed by comparison of the tibiotarsus/humerus ratios (Fig. 5b).

The relative length of the leg in these geese results principally from different combinations of tibiotarsal and tarsometatarsal lengths (Table 3), since their femora seem to be comparatively uniform in relative size. In long-legged *Anser caerulescens* (and *A. rossii*, which, being relatively similar in most respects is omitted from further comparisons), the tibiotarsus and tarsometatarsus are both long. In short-legged *Branta canadensis* and *A. albifrons* (and probably in *A. anser* and *A. fabalis*), both elements are short. The fossil also has a short leg, but this results from a very short tibiotarsus offsetting

Table 3. Differences and their significances for each comparison of the relative length of the tibiotarsus (lower left) and tarsometatarsus (upper right) among *Anser thompsoni* and several Recent geese.*

	<i>Anser thompsoni</i>	<i>Anser caerulescens</i>	<i>Branta canadensis</i>	<i>Anser albifrons</i>
<i>Anser thompsoni</i>	—	longer n.s.	shorter $0.02 < p < 0.05$	shorter $0.01 < p < 0.02$
<i>Anser caerulescens</i>	shorter $p < 0.001$	—	shorter $p < 0.001$	shorter $p < 0.001$
<i>Branta canadensis</i>	shorter n.s.	longer $p < 0.001$	—	shorter n.s.
<i>Anser albifrons</i>	shorter n.s.	longer $p < 0.001$	shorter n.s.	—

* Read down (e.g., the tibiotarsus of *A. thompsoni* is relatively shorter than that of *A. caerulescens*, etc.). The letters n.s. stand for not significant.

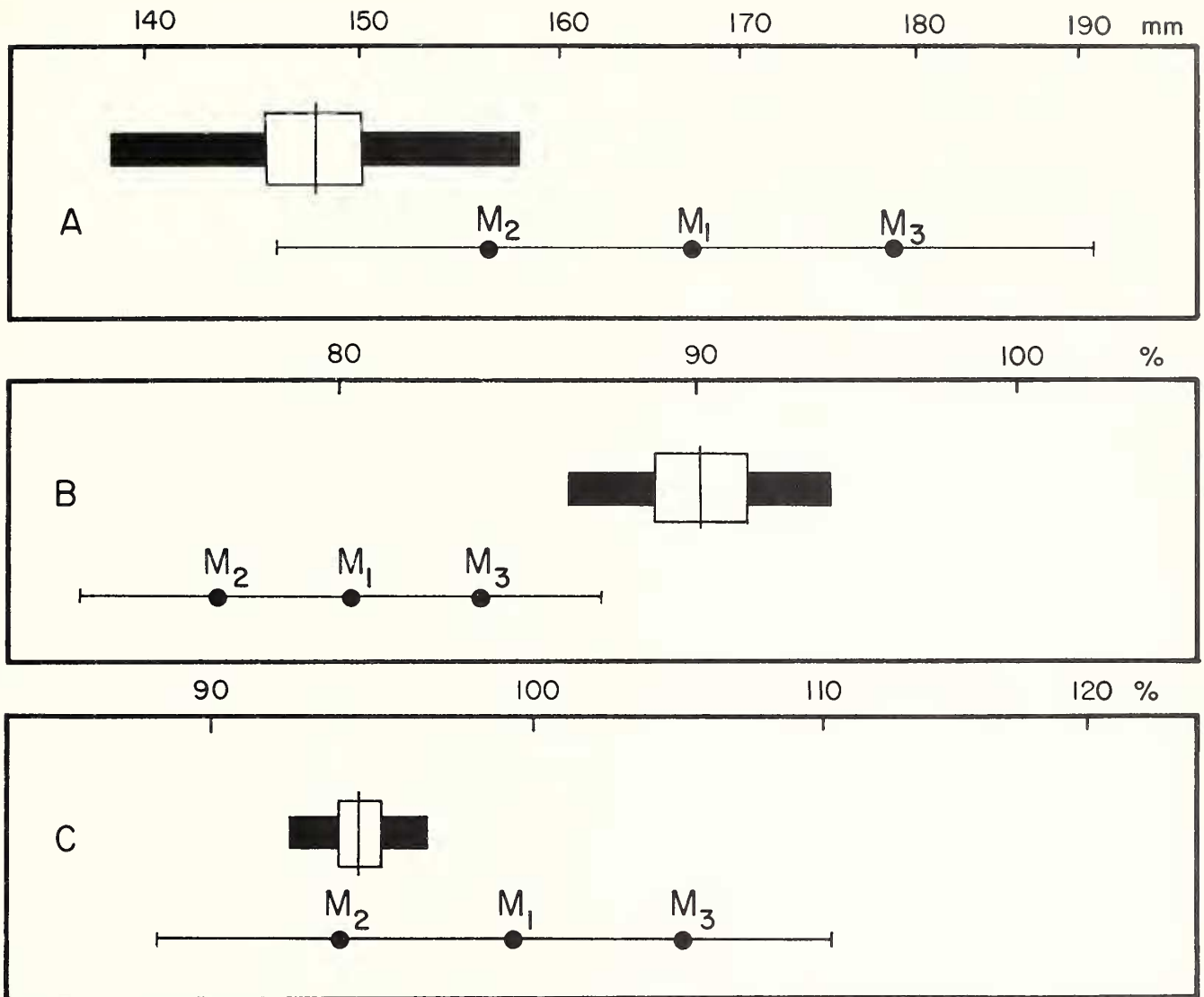


Figure 5. Some statistics of *Anser thompsoni* and Recent taxa. A, length of humerus, compared with *A. caerulescens caerulescens* males. B, length of tibiotarsus/length of humerus, compared with *A. c. caerulescens*. C, length of ulna (estimated)/length of humerus, compared with *Branta canadensis*. For Recent taxa: white boxes = mean $\pm$ 2 standard errors; black rectangles = mean $\pm$ 2 standard deviations; vertical lines = means. For *A. thompsoni* new species, M_1 , M_2 , and M_3 = theoretical means with the holotype regarded, respectively, as average, 2σ below, and 2σ above the mean (σ inferred from *A. caerulescens*); horizontal line = $M_1 \pm 4\sigma$. The horizontal scale is logarithmic. For details see text.

the lesser effect of a comparatively long tarsometatarsus. In Table 3 and the text, probabilities are those resulting from Student's *t* test of the difference between means (for its variant formula for comparing single specimens with samples, see Simpson, Roe, and Lewontin 1960:182–183; or Sokal and Rohlf 1969:224–225).

It is difficult to assess these differences in a functional context with present knowledge. Our initial tendency to regard the long legs of the Snow Goose as an adaptation for grazing per se was dampened by indications (Palmer 1976:150, 233) that the Snow Goose is more addicted than the Canada Goose (and probably more than the White-fronted Goose) to aquatic feeding. We now hazard the guess that short legs in geese are related to grazing on comparatively bare ground or in low cover on land or in shallow water, where a long neck, as in *Branta canadensis*, usefully increases the area covered. Longer

legs appear better suited to marshy substrates and higher cover. *Anser thompsoni* seems to belong in the first category.

2. Relative lengths of forelimb elements. *Anser caerulescens* and *A. rossii* have long ulnae in relation to their humeri (Verheyen 1955b:10–12). In our samples this relative difference in length is highly significant when either is compared with *Branta canadensis* ($p < 0.001$). *Anser albifrons* has an intermediate ulna/humerus index, but its ulna, relatively, is still significantly shorter than that of the Snow Goose ($0.01 < p < 0.02$). With its long ulna, *A. thompsoni* resembles *A. caerulescens*, in comparison (Fig. 5c) with *B. canadensis* ($0.001 < p < 0.01$). The length of the ulna of *A. thompsoni* is approximate, but even if it were 2 mm shorter than estimated, or 164 mm, it would still be significantly longer than that of *B. canadensis* ($p < 0.02$).

The carpometacarpus of *Anser thompsoni* is also relatively

longer than those of Recent geese considered, which are rather uniform in this regard. Compared with *A. caerulescens*, this difference in length is significant ($0.01 < p < 0.02$).

Proportions in wing elements are related to the mechanics of flight in ways that are often obscure. Further complications are introduced by feather geometry, which is little studied in present-day forms and unknown in nearly all fossils (see Engels 1941 on hawks and Fisher 1946 on New World vultures).

All anseriforms, however, are comparatively short-winged and heavily wing-loaded, conditions resulting in rapid, flapping flight. Their wings are therefore in the same general category (Böker 1927) as those of falcons and swallows ("Schwirrflug"). With this wing-form, speed and maneuverability are evidently increased by lengthening of the outer elements, particularly those of the hand, and the primary feathers. In geese, this would mean a more duck-like wing. (Mengel, after many hours of field observation, thinks that the Snow Goose is more agile and maneuverable aloft than the Canada Goose.) Further, the proximal extension and relative length of the extensor attachment of the process of metacarpal I in *Anser thompsoni*, in comparison with all Recent geese, are features associated with maneuverability and quick response. These features are not as well adapted to sustained heavy work loads (Fisher 1946:559), however, as the more distally situated and elongate processes of Recent geese and, particularly, swans.

From these considerations we conjecture that *A. thompsoni* was probably a rapid and, for its size, a comparatively maneuverable flier. Its skeleton, as noted above, also appears to have been less pneumatic than those of the modern geese we have studied. We hesitate to assess the significance of this, particularly since Prange et al. (1979) have recently posed searching questions concerning the whole relationship of flight and pneumaticity. The very small furcula of *A. thompsoni* is also of interest here because a very appreciable portion of *M. pectoralis major*, the principal adductor of the wing, inserts on this element. Conceivably this late Pliocene goose did not perform annual migrations as long as those of Recent geese. If this is true, the features discussed above may somehow be related to long distance migratory flight.

3. Cranial proportions. The type of *Anser thompsoni* is very short-billed. Although the ratio of bill length to total head length is rather variable in Recent geese, the difference between this ratio in the fossil and its mean in the Recent Snow Goose is very significant ($0.01 < p < 0.02$). This, together with inspection of the values for other Recent geese supports the supposition that *A. thompsoni* was indeed a short-billed goose. The only comparably short-billed Recent *Anser* is the little *A. canagicus*, or Emperor Goose, a tidal flat grazer and grubber of the Bering Sea region. We are not prepared to consider the possible functional significance of these facts.

SUMMATION

While our total picture of *Anser thompsoni* is blurred by imperfect preservation, it is still the most complete of any known fossil goose. This bird seems to have been a big, dumpy, short-legged, rather long-winged, short-billed *Anser*, larger than a Snow Goose but resembling that species in flight silhouette and maneuverability. In size certainly, and in general appearance probably, it resembled the Old World Greylag (*A. anser*). It may not have been highly migratory.

The proportional configurations of Recent geese are rather variable and doubtless represent subtle adaptations to behavioral modes that could easily be rather plastic. *Anser thompsoni* displays a unique and perhaps rather specialized combination, particularly in its short tibiotarsal-long tarsometatarsal combination.

The carpometacarpus is also intriguing, specifically the shape of the process of metacarpal I, which distinguishes *Anser thompsoni* from at least the Recent species of both *Anser* and *Branta*, and which we suspect may be the primitive condition for geese. Whether or not improved knowledge of fossil geese supports this position, we suspect that further information on this and other characters will require some systematic realignments consistent with the distribution of shared-derived characters when, and if, these characters can be identified.

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